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Abstract: • **Premise of the study:** Investigations of inflorescence architecture offer insight into the evolution of an astounding array of reproductive shoot systems in the angiosperms, as well as the potential to genetically manipulate these branching patterns to improve crop yield and enhance the aesthetics of horticultural species. The diversity of inflorescences in the economically important family Oleaceae was studied from a comparative developmental point of view for the first time, based on species of seven genera (Chionanthus, Fontanesia, Fraxinus, Jasminum, Ligustrum, Olea, Syringa). • **Methods:** Series of developmental stages of chemically fixed inflorescences were studied with epi-illumination light microscopy. • **Key results:** All taxa studied have inflorescences with terminal flowers. The inflorescences are mostly panicles, but in some cases thyrsoids or compound botryoids. Phyllotaxis of the flower-subtending bracts is mostly decussate, rarely tricussate (Fraxinus) or spiral (Jasminum). Accessory flowers or accessory inflorescences, almost unknown in Oleaceae as yet, were found in two genera. In Syringa, common bract-flower primordia are formed by a delay in early bract development compared to flower development. Such a delay is also expressed by the loss of bracts in the distal part of inflorescence branches in Syringa and Chionanthus. • **Conclusions:** Significant variation in branching pattern and phyllotaxy was observed among the studied species of Oleaceae. The suppression of bracts and formation of accessory flowers were found as special features of inflorescence ontogeny. The occurrence of accessory flowers and accessory partial inflorescences is interesting from the point of view of dense and flower-rich inflorescences in ornamental species.

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COMPARATIVE STUDY OF INFLORESCENCE DEVELOPMENT IN OLEACEAE¹

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- *Premise of the study:* Investigations of inflorescence architecture offer insight into the evolution of an astounding array of reproductive shoot systems in the angiosperms, as well as the potential to genetically manipulate these branching patterns to improve crop yield and enhance the aesthetics of horticultural species. The diversity of inflorescences in the economically important family Oleaceae was studied from a comparative developmental point of view for the first time, based on species of seven genera (*Chionanthus*, *Fontanesia*, *Fraxinus*, *Jasminum*, *Ligustrum*, *Olea*, *Syringa*).
- *Methods:* Series of developmental stages of chemically fixed inflorescences were studied with epi-illumination light microscopy.
- *Key results:* All taxa studied have inflorescences with terminal flowers. The inflorescences are mostly panicles, but in some cases thyrsoids or compound botryoids. Phyllotaxis of the flower-subtending bracts is mostly decussate, rarely tricusate (*Fraxinus*) or spiral (*Jasminum*). Accessory flowers or accessory inflorescences, almost unknown in Oleaceae as yet, were found in two genera. In *Syringa*, common bract-flower primordia are formed by a delay in early bract development compared to flower development. Such a delay is also expressed by the loss of bracts in the distal part of inflorescence branches in *Syringa* and *Chionanthus*.
- *Conclusions:* Significant variation in branching pattern and phyllotaxy was observed among the studied species of Oleaceae. The suppression of bracts and formation of accessory flowers were found as special features of inflorescence ontogeny. The occurrence of accessory flowers and accessory partial inflorescences is interesting from the point of view of dense and flower-rich inflorescences in ornamental species.

Key words: accessory flowers; accessory inflorescences; branching pattern; epi-illumination microscopy; inflorescence development; Oleaceae; phyllotaxis.

In the past two decades, the importance of developmental data has been reestablished, and investigators in many disciplines of plant biology, for example morphology, horticulture, genetics, and systematics use developmental information in their fields (Endress, 2006; Dadpour et al., 2011; Naghiloo et al., 2012). Certainly, developmental studies are of great interest in phylogenetic analyses, because unlike other data used in phylogeny, they are applicable either as a source of raw data (i.e., new characters) or as a means of evaluating and testing other characters by assessing the homology of the various character states. On the other hand, comparative developmental morphology plays a crucial role in evolutionary studies by adding a temporal component, which is not available when only mature structures are analyzed.

Information derived from the study of the early stages of inflorescence development utilizing three-dimensional microscopic techniques is more decisive than that from the study of mature inflorescences. In some cases, wrong interpretations

of the ramification patterns based on mature inflorescences have been corrected with developmental studies, such as in Solanaceae, in which it may be difficult to distinguish between main and lateral axes at maturity (e.g., Huber, 1980; Welty et al., 2007). In addition, to convincingly show the presence of accessory flowers or accessory partial inflorescences, developmental studies are necessary because flower-subtending bracts may disappear early by abscission (Weber et al., 1992).

While there have been some detailed developmental studies of inflorescences, (e.g., Harris, 1995; Sokoloff et al., 2007; Bull-Hereñu and Classen-Bockhoff, 2011; Feng et al., 2011; Pozner et al., 2012; see also Singer, 2006), such studies have received less attention than studies of comparative floral development. Understanding the developmental basis underlying the evolution of inflorescence architecture could shed light on the role of inflorescence architecture in pollination and reproduction. Here we examine inflorescence development in representative members of the Oleaceae.

The family Oleaceae comprises approximately 25 genera and 600 species (Green, 2004). Recent molecular studies have placed Oleaceae in Lamiales as one of its first-diverging families (Oxelman et al., 1999, 2005; Olmstead et al., 2001; Stevens, 2001 onward; Tank et al., 2006). The members of the family are trees, shrubs, or woody climbers with almost worldwide distribution. Oleaceae are an economically well-known family containing important crops (olive), ornamentals (lilac, *Forsythia*, jasmine, privet), and timber-producing plants (*Fraxinus*). Most

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Oleaceae produce polysymmetric flowers with tetramerous calyx and corolla and dimerous androecium and gynoecium (Sehr and Weber, 2009; Dadpour et al., 2011). Troll (1969) provided a comparative study on inflorescences of some genera of the tribes Forsythieae and Oleaeae, but without considering developmental aspects. According to Green (2004), and in his terminology, inflorescences vary from simple cymes to thyrsoids and panicles.

Given the recent developments in phylogenetics and developmental biology of Oleaceae and the pivotal role of inflorescences in the function and diversification of plants, it is time to

look at inflorescences from a new perspective. In this study, an attempt is made to clarify the developmental pathways of different types of inflorescences in Oleaceae. Accordingly, seven genera have been investigated, covering all tribes recognized in the phylogenetic study by Wallander and Albert (2000), except Forsythieae and Myxopyreae. To characterize the inflorescences, we use the terminology discussed in Weberling and Troll (1998) and Endress (2010) (Box 1).

The objectives of this work were (1) to characterize inflorescence structure and development in representative tribes of Oleaceae based on three-dimensional microscopic studies,

BRANCHING PATTERNS

Racemose branching

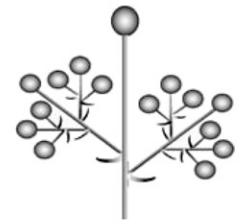
The main (first-order) axis (branch) has an unlimited number of lateral (second-order) branches, but there are no higher order branches. The main (first-order) axis can ultimately be terminated by a flower or remain open.



Racemose

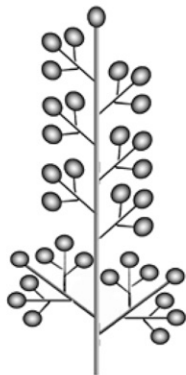
Cymose branching

The first-order axis (branch) never has more than two second-order axes (branches) and never more than two extrafloral leaves (phyllomes); however, the second-order branches can branch one or more times in the same way. All branches are commonly terminated by a flower, but there are also cases in which the first-order branch is without a flower. Cymose units with two lateral branches are termed dichasial, and those with single lateral branches are termed monochasial.



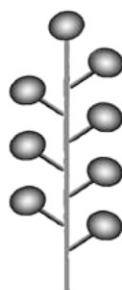
Cymose

INFLORESCENCES



Thyrsoid

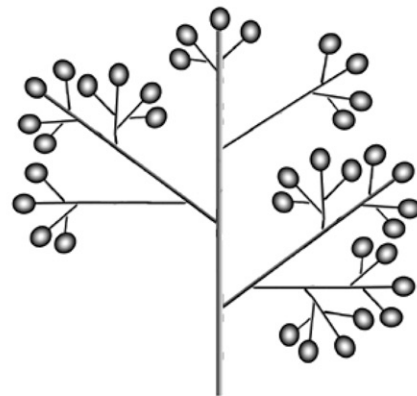
Thyrse/Thyrsoid An inflorescence with racemose primary branching and cymose secondary branching is a thyrse if the primary branch is not terminated by a flower (indeterminate) and a thyrsoid if the primary branch is terminated by a flower (determinate).



Botryoid

Botryum/Botryoid

An inflorescence with racemose branching is a botryum if the primary branch is not terminated by a flower (indeterminate), and a botryoid if the primary branch is terminated by a flower (determinate).



Panicle

Panicle A panicle does not have the limitations of racemose and cymose branching patterns; neither the number of branching orders nor the number of flowers within one branching order are limited. Branching is commonly richest at or close to the base of the main branch and becomes successively less rich moving up the main branch. Each branch is terminated by a flower.

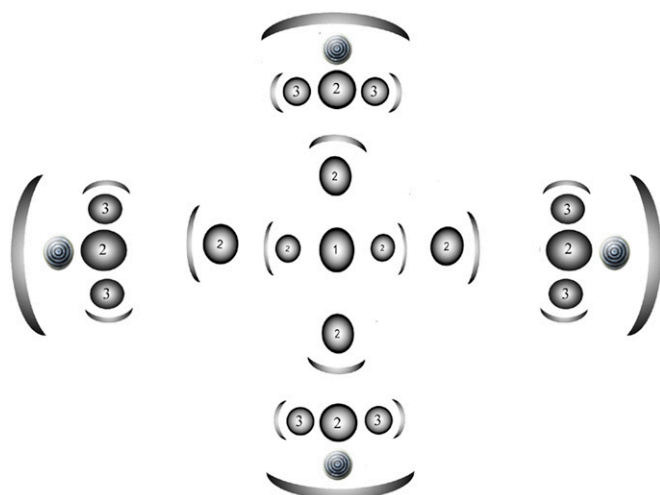


Fig. 1. *Fontanesia phillyreoides*. Inflorescence diagram. Flowers are numbered according to their branching orders. Flowers without numbers are accessory flowers.

(2) to identify potential new characters to include in evolutionary studies, such as the presence of accessory flowers or accessory partial inflorescences, which are known from some other families of Lamiales, (3) to demonstrate potential developmental processes responsible for inflorescence diversity in the family, and (4) to discuss implications of the results in relation to taxonomy within the family. At present, an evaluation of evolutionary processes in the diversification of the inflorescences within the family is only possible to a limited degree as the phylogenetic resolution between the genera is still poor.

MATERIALS AND METHODS

Inflorescences at different developmental stages were collected from the following species: *Chionanthus virginicus* L., P. K. Endress 11-1, cultivated, Botanic Garden of the University of Zurich, Switzerland; *Fontanesia phillyreoides* Labill., P. K. Endress 11-2, cultivated, Botanic Garden, University of Zurich, Switzerland; *Fraxinus excelsior* L., M. R. Dadpour Tbmed-Sth532, cultivated, University of Tabriz, Iran; *Jasminum fruticans* L., S. Nikzat Tbmed-Sth530, cultivated, University of Tabriz, Iran; *Ligustrum vulgare* L., M. R.

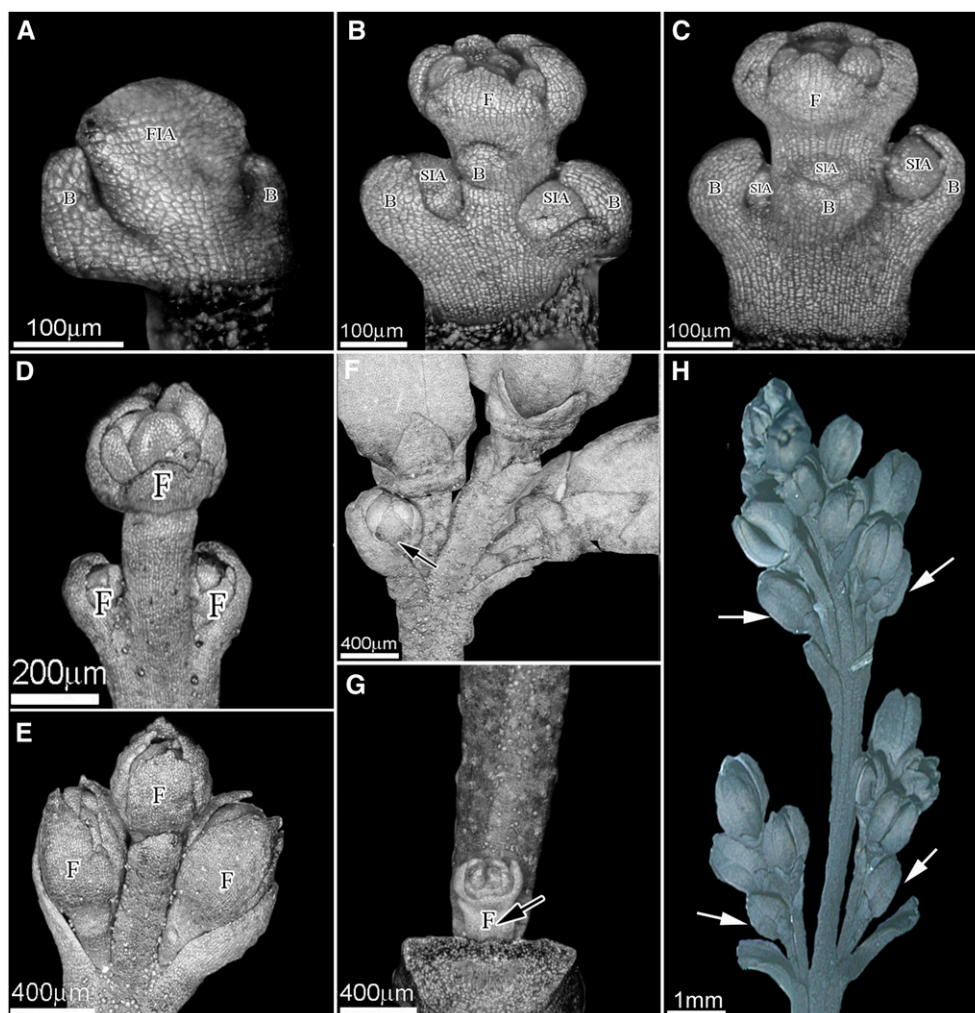


Fig. 2. *Fontanesia phillyreoides*. Inflorescence development. (A) The first-order inflorescence apex (FIA) produces two lateral bracts and converts into a flower. (B) Secondary-order inflorescence apices (SIAs) are initiated in the axil of bracts. (C) Initiation of bracts and SIAs follows in decussate pattern. (D, E) Each SIA produces two lateral flowers and terminates in a flower. (F, G) Accessory flowers accompanying cymes are produced (arrows). (H) A developed inflorescence showing the accessory flowers in lower branches (arrows). Abbreviations: B, bract; F, flower.

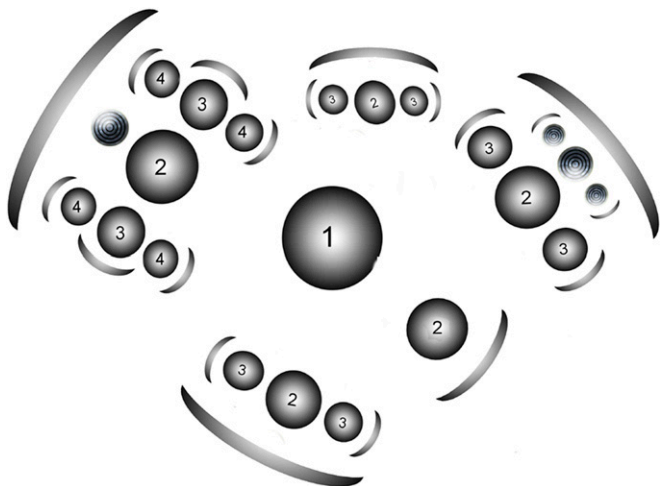


Fig. 3. *Jasminum fruticans*. Inflorescence diagram. Flowers are numbered according to their branching orders. Flowers without number are accessory flowers or part of accessory inflorescences.

Dadpour Tbzmed-Sth533, cultivated, University of Tabriz, Iran; *Olea europaea* L., *S. Nikzat Tbzmed-Sth531*, cultivated, Ghaemshahr, Iran; *Syringa vulgaris* L., *M. R. Dadpour Tbzmed-Sth534*, cultivated, University of Tabriz, Iran.

The fixed material is stored at the Department of Horticultural Sciences, Faculty of Agriculture, University of Tabriz, Iran. The materials were immediately fixed in FAA (5 parts formalin, 5 parts glacial acetic acid, 90 parts 50% ethanol). After a fixation period of 24 h, the samples were rinsed, dehydrated in 70% ethanol, and further dehydrated in 95% ethanol before staining with alcohol-soluble nigrosin (0.4% nigrosin in 95% ethanol) for at least 2 d according to the method reported by Charlton et al. (1989). The specimens were washed in 95% ethanol before microscopic study.

Epi-illumination light microscopy—Prepared samples were observed with a Nikon E600 reflected light microscope (Nikon, Tokyo, Japan) in dark-field mode. Image (z-stack) acquisition was performed with a Nikon DXM1200F high-resolution digital camera. For this purpose, series of consecutive images from different focal planes of the sample were taken and then superimposed automatically to improve the depth of focus by using Image J 1.41 software (freely available from National Institutes of Health, <http://rsbweb.nih.gov/ij/>) in accordance with Dadpour et al. (2008). Outputs from the z-stack acquisition were trimmed and saved as TIF-format images.

RESULTS

Fontanesia—The flowers of *Fontanesia phillyreoides* are borne in thyrsoid inflorescences (Fig. 1). The first-order inflorescence apex (FIA) produces two lateral bracts and then terminates in a flower (Fig. 2A). Compared to other studied taxa, termination of the main inflorescence apex occurs very early just after production of the first bracts (Fig. 2A). Subsequently, two second-order inflorescence apices (SIAs) appear in the axil of bracts, while the formation of SIAs and their preceding bracts continues decussately (Fig. 2B, C). Each SIA then produces two third-order inflorescence apices (TIAs) and is converted into a flower (Fig. 2D, E). However, in the uppermost branch, the SIA terminates in a flower without further branching (Fig. 2H). Accessory flowers are initiated at the base of all lower branches (Fig. 2F, G). As a consequence, in lower branches of a developed inflorescence, flowers are in clusters of four (Fig. 2H).

Jasminum—The inflorescences of *Jasminum fruticans* are thyrsoids, with a determinate main inflorescence axis carrying

3–5 cymosely branched second-order inflorescence axes (Fig. 3). After transition to flowering, the FIA produces 3–5 helically arranged primary bracts, and then SIAs are initiated in the axil of each bract (Fig. 4A). Concurrently, the FIA converts into a flower (Fig. 4B). After successive initiation of two opposite bracts and the flowers (or TIAs) in their axils, SIAs are converted into a terminal flower (Fig. 4C, D). In lower branches, flowers are in clusters of three or more, while in the uppermost branch further branching does not occur and it is reduced to a single flower (Fig. 4G). With the progression of development, the lower lateral branches remain small and are surpassed in growth by the upper ones (Fig. 4E–H). This unequal growth gives the wrong impression of a basipetal development. The subtending bracts of the uppermost lateral flowers remain small (Fig. 4I, J). Accessory flowers or partial inflorescences appear at the base of the secondary lateral branches (Fig. 4K–N). However in *J. fruticans*, unlike *Fontanesia phillyreoides*, the formation of accessory flowers and inflorescences does not follow a regular pattern (Fig. 3).

Ligustrum—The inflorescences of *Ligustrum vulgare* are panicles (approaching compound botryoids or compound thyrsoids) with more than 20 second-order inflorescence branches and 10 third-order inflorescence branches (Fig. 5). The FIA produces decussately arranged bracts, each of which subtending a SIA (Fig. 6A–D). Each SIA enlarges and produces bracts subtending TIAs with a regular decussate phyllotaxis (Fig. 7A–J). Production of higher-order inflorescence apices continues up to termination of the main inflorescence apex activity (Fig. 6E–G). The basalmost branches undergo further branching and encompass several dichasial units. After formation of about 20 SIA, the main inflorescence apex terminates in a flower (Fig. 6H, I). Concurrently, branching stops in all branches, and the inflorescence apices of all orders convert into flowers (Fig. 7K, L). In upper branches, which have a shorter time for branching before the meristematic activity ceases, branching becomes successively less rich (Fig. 6H, I). Uppermost branches may be reduced to a flower. However, even in these flowers, vestigial bracts are visible, indicating that branching begins with the formation of opposite bracts, but the meristematic activity ceases before formation of new branches in the axil of these bracts (Fig. 7M, N, P). In some cases, duration of meristematic activity is somewhat longer, resulting in the formation of only one lateral branch (Fig. 7O).

Syringa—Like *Ligustrum vulgare*, the inflorescences of *Syringa vulgaris* are panicles (approaching compound botryoids or compound thyrsoids) with more than 20 second-order inflorescence branches and 10 third-order inflorescence branches (Fig. 8). The FIA produces decussately arranged bracts, which subtend second-order inflorescence apices (SIAs) (Fig. 9A). Each SIA enlarges and produces a pair of common primordia in lateral position, each of which develops into a bract and a TIA (Fig. 9B, 9C, 10A–C). Production of bracts and TIAs continues in a decussate pattern (Fig. 10D–F). The progression of branching in lateral position is faster than in median position. Each TIA also may continue branching and produce fourth-order branches (FOA) (Fig. 10E, F). The basal branches undergo further branching and toward the upper ones branching becomes successively less rich (Fig. 9D–F). Except for the first-order bracts, the bracts cease growth after initiation, and no bract is visible in developed inflorescences (Fig. 10G, H). Thus, there

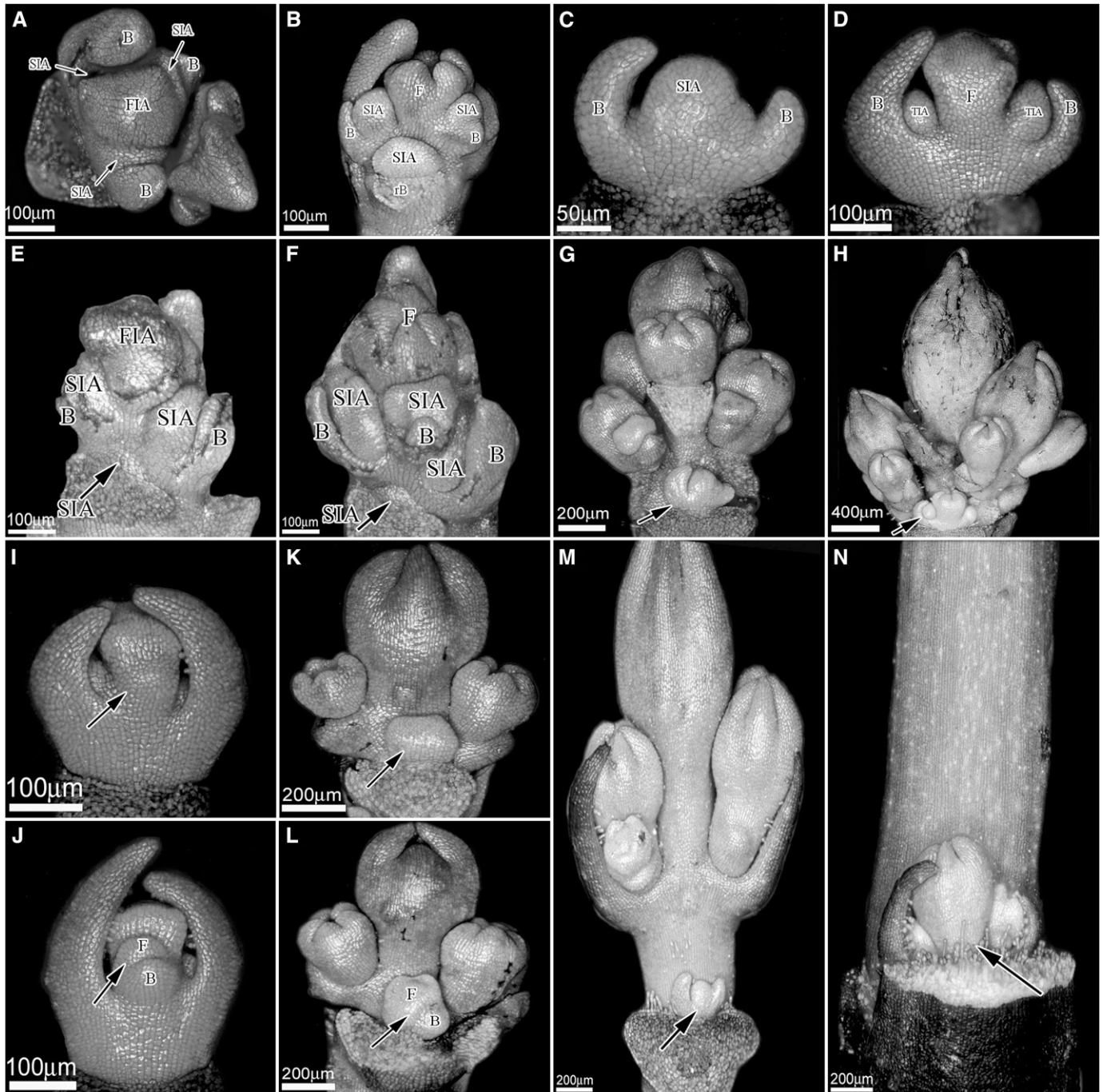


Fig. 4. *Jasminum fruticans*. Inflorescence development. (A, B) The first-order inflorescence apex (FIA) produces bracts and second-order inflorescence apices (SIAs) spirally. (C) The SIA produces two bracts in lateral position. (D) Third-order inflorescence apices (TIAs) form in the axil of bracts, and the SIA terminates in a flower. (E–H) Different developmental stages showing retarded formation and development of lowermost branches (arrows). (I–N) Lateral inflorescence units (SIAs). (I, J) Upper lateral flower forming. (K, L) Accessory flower (arrow) forming in axil of bract, accompanying a cyme (in image L with lateral bract [prophyll]). (M, N) Accessory partial inflorescence appearing in the axil of a bract, accompanying a cyme (arrows). *Abbreviations*: B, bract; F, flower.

appear to be clusters of flowers, each cluster subtended by a single bract (Fig. 9G, H).

Fraxinus—Inflorescences of *Fraxinus excelsior* are markedly different from those of the other studied taxa in both branching pattern and phyllotaxis. The pattern of branching is only racemose,

with the main (first-order) axis having a variable number of lateral (second-order) branches, but there are no higher-order branches (Fig. 11). The main inflorescence apex produces tricussately arranged primary bracts subtending SIAs, and then is converted into a flower (Fig. 12A–C). Each SIA also terminates in a flower and further branching does not occur (Fig. 12D–G).

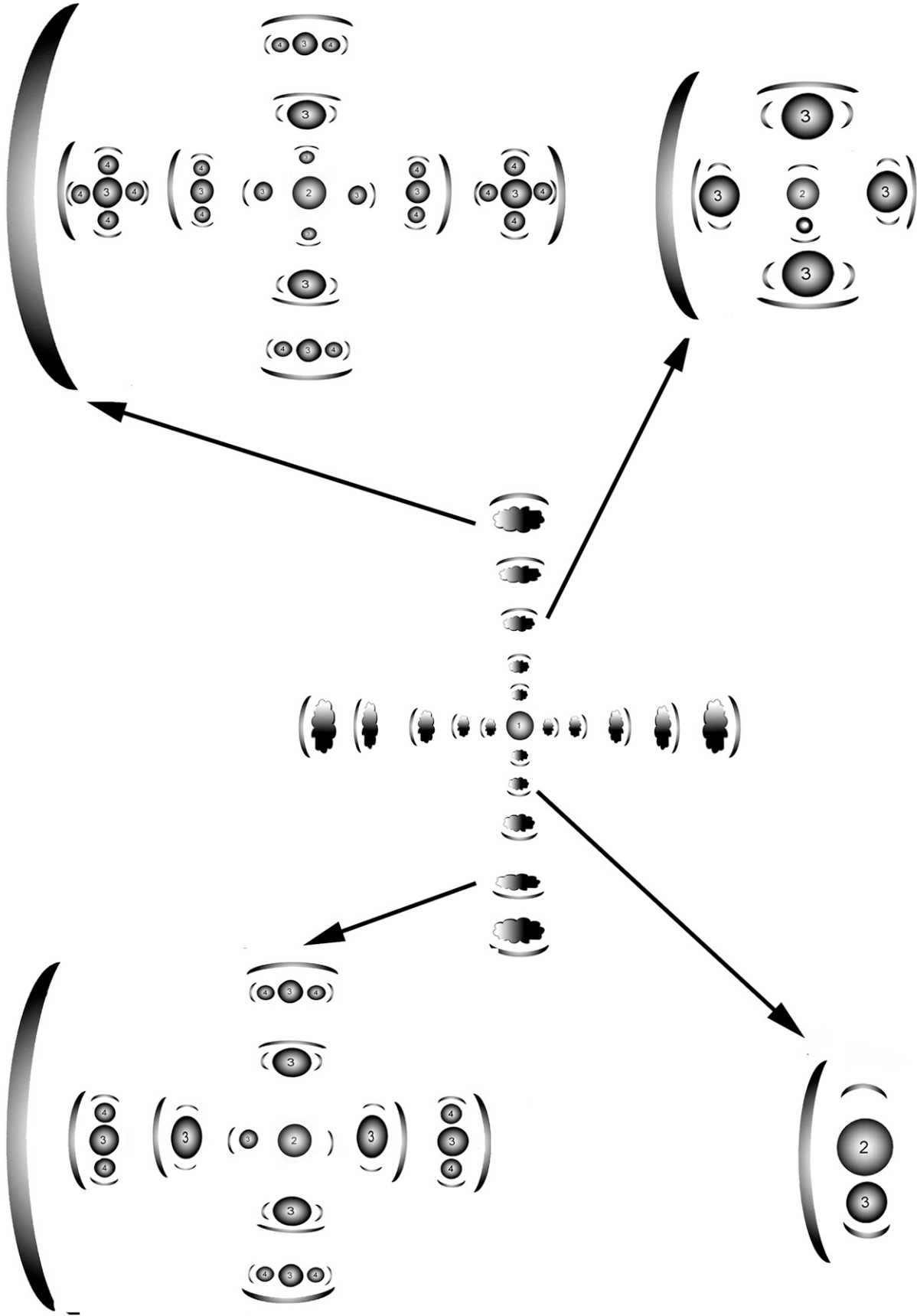


Fig. 5. *Ligustrum vulgare*. Inflorescence diagram. Flowers are numbered according to their branching orders.

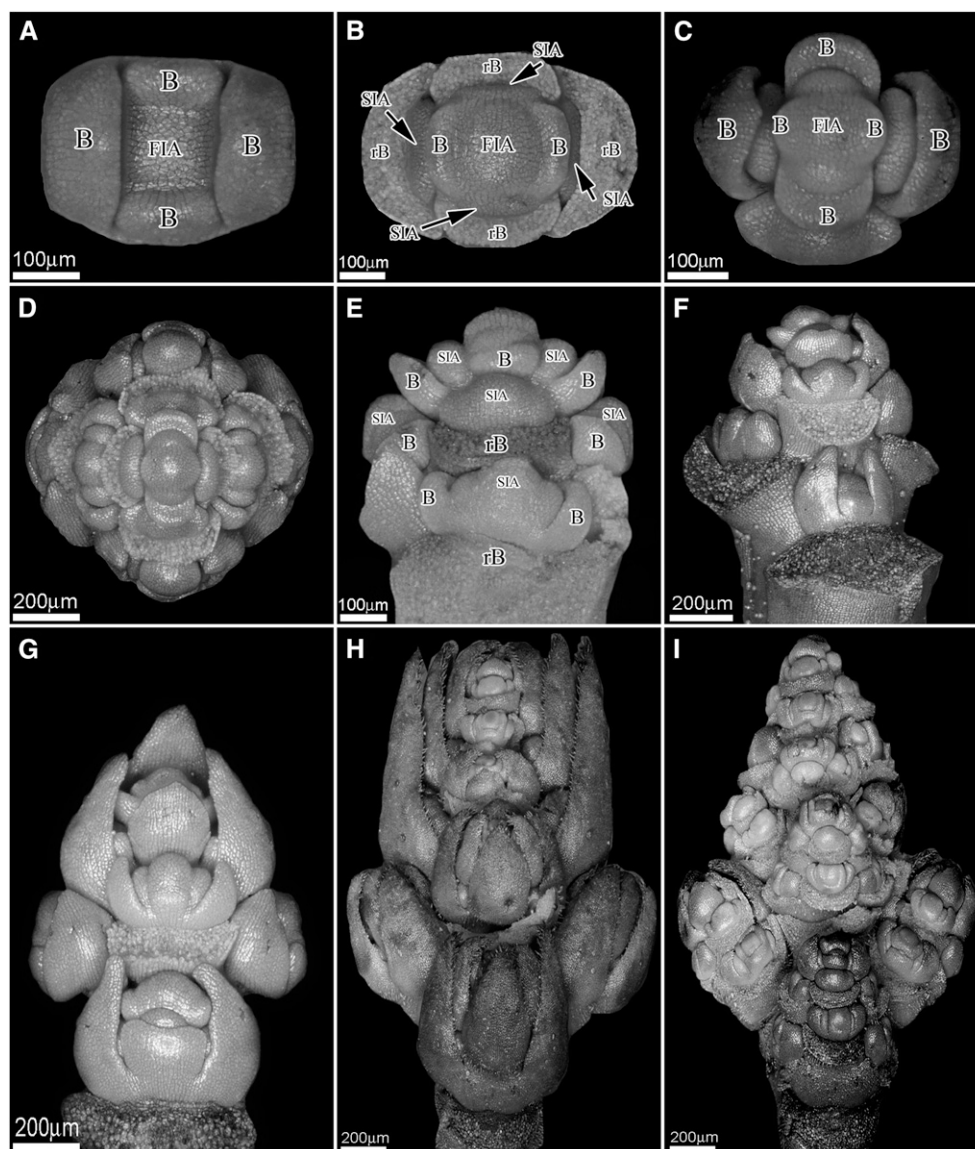


Fig. 6. *Ligustrum vulgare*. Inflorescence branching. (A) The first-order inflorescence apex (FIA) produces decussate bracts. (B) Second-order inflorescence apices (SIAs) are initiated in the axil of bracts. (C, D) The FIA continues to produce bracts and SIAs. (E–G) Side views of inflorescences showing progression of branching. (H, I) The FIA terminates in a flower in fully developed inflorescences. Degree of branching in lower branches is richer than in upper branches. Abbreviation: B, bract.

Olea—In *Olea europaea*, the inflorescences are panicles (approaching compound botryoids or compound thyrsoids) like in *Syringa vulgaris* and *Ligustrum vulgare*, but branching is less rich (Fig. 13). The FIA produces decussately arranged bracts, in the axil of which the SIAs are initiated (Fig. 14A, B). After formation of five SIAs, branching ceases. Meanwhile, the lowermost two pairs of second-order branches produce 2–4 decussately arranged third-order bracts and the TIAs they subtend (Fig. 14C–F). The upper second-order branches do not produce any lateral TIAs, and each is converted into a single flower (Fig. 14G).

Chionanthus—Although the early stages of inflorescence development in *Chionanthus virginicus* were not available for study, it can be stated that the inflorescence is a thyrsoid, with 8–10 cymosely branched second-order inflorescence

branches (Figs. 15, 16A). Except for uppermost branches, each SIA produces two lateral flowers (TIAs) and then is converted into a terminal flower (Fig. 16B, C). Interestingly, like in *Syringa vulgaris*, in the majority of branches there are no bracts on second-order branches (Fig. 16B, D, H). However, in some cases reduced bracts are observed at the base of third-order branches (Fig. 16E–G).

DISCUSSION

To understand the diversity of inflorescences in Oleaceae, we need to address some basics of the ramification patterns in the Discussion. New features characteristic for part of the family are the developmental disappearance of subtending bracts and the occurrence of accessory flowers and accessory inflorescences.

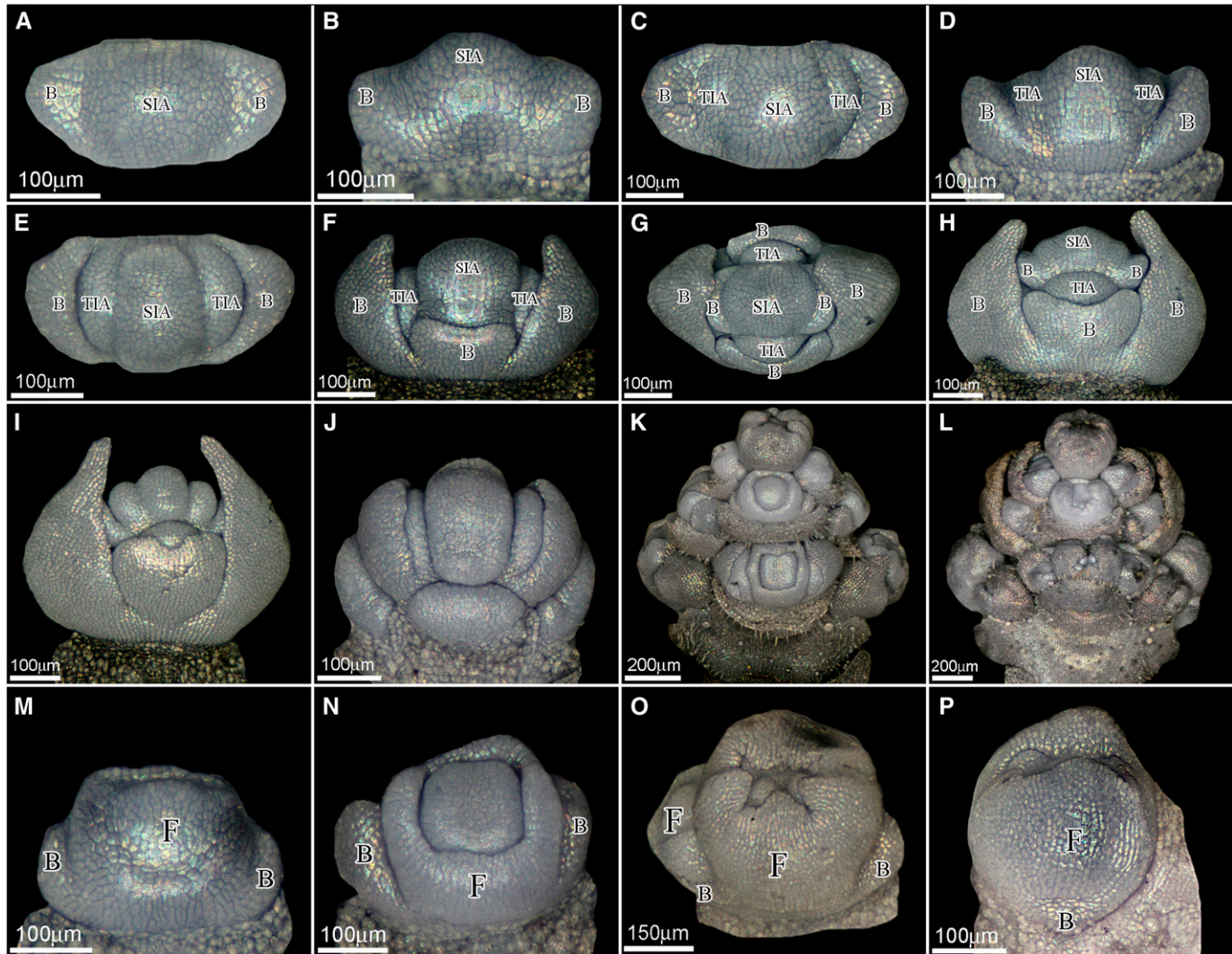


Fig. 7. *Ligustrum vulgare*. Branching of second-order inflorescence apices (SIAs). (A, B) Apical and side views showing the production of bracts on lateral sides of the SIA. (C, D) Third-order inflorescence apices (TIAs) are formed in the axil of bracts. (E–J) Formation of bracts and TIAs proceeds decussately. (K, L) Branching ceases, and the apices of branches of all orders convert into a flower. (M, N) Two bracts produced on lateral sides of an upper branch, but no TIA is initiated in their axil. (O) Side view of an upper branch with two bracts, one of them subtending a flower. (P) A reduced bract (arrow) in the uppermost branch, with a flower in its axil. Abbreviations: B, bract; F, flower.

Branching patterns—The basic branching patterns (racemose and cymose) that occur in inflorescences and the most common simple inflorescence types (thyrsoid, botryoid, and panicle) are shown in Box 1 (for a review of these branching patterns and inflorescence forms, see Endress, 2010). In compound thyrsoids, the primary lateral branches are not cymes but thyrsoids, and in compound botryoids, the lateral branches are not flowers but botryoids. What was called panicles in *Fraxinus*, *Ligustrum*, and *Syringa* by Troll (1969) has almost the configuration of compound botryoids because further branching in the second-order branches is poor and in the upper branches often lacking. This branching pattern is also present in *Olea* (not studied in Troll, 1969).

Various types of branching patterns were found in the studied taxa of Oleaceae. *Jasminum fruticans*, *Fontanesia phillyreoides*, and *Chionanthus virginicus* produce thyrsoids. From a survey with good illustrations of mature inflorescences, it

appears that almost all species of *Jasminum* have thyrsoids, only a few have botryoids (Green and Miller, 2009). With the increase in flower number in *Syringa vulgaris* and *Ligustrum vulgare*, branching changes to a panicle pattern. This pattern also occurs in *Fraxinus ornus*, and some inflorescences of *F. excelsior* (Troll, 1969). These thyrsoids and panicles in Oleaceae have a slender conical shape because the amount of branching tends to slightly decrease from the base to the top. The material of *F. excelsior* studied here is racemose (the inflorescences are botryoids) with only first-order and a variable number of second-order branches.

Bracts—Branching occurs from the axil of a bract or a foliage leaf (pheryphyll) that subtends the lateral branch. In most of the studied taxa, after initiation of opposite bracts by the main axis, lateral buds are formed in the axil of these bracts and develop

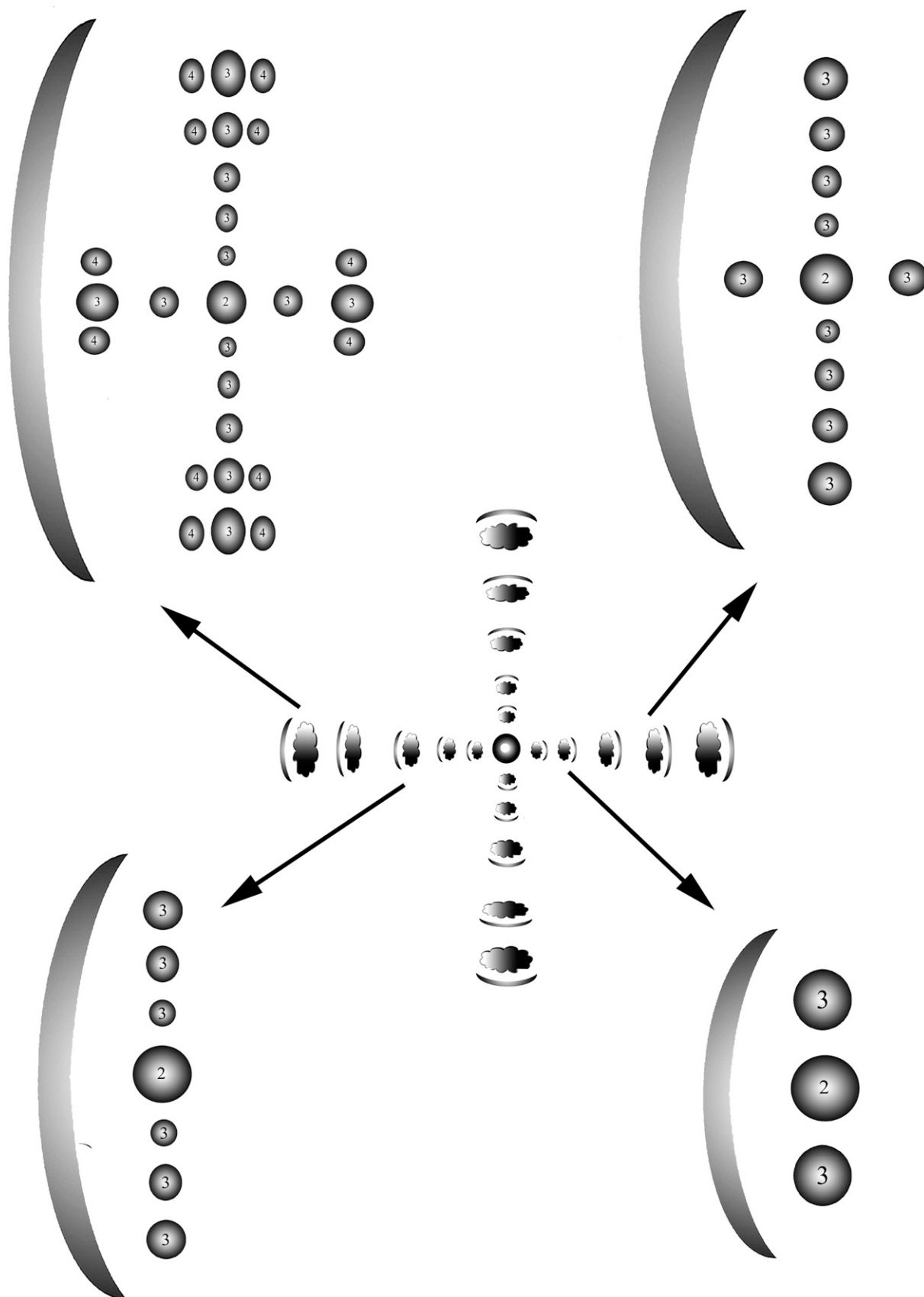


Fig. 8. *Syringa vulgaris*. Inflorescence diagram. Flowers are numbered according to their branching orders.

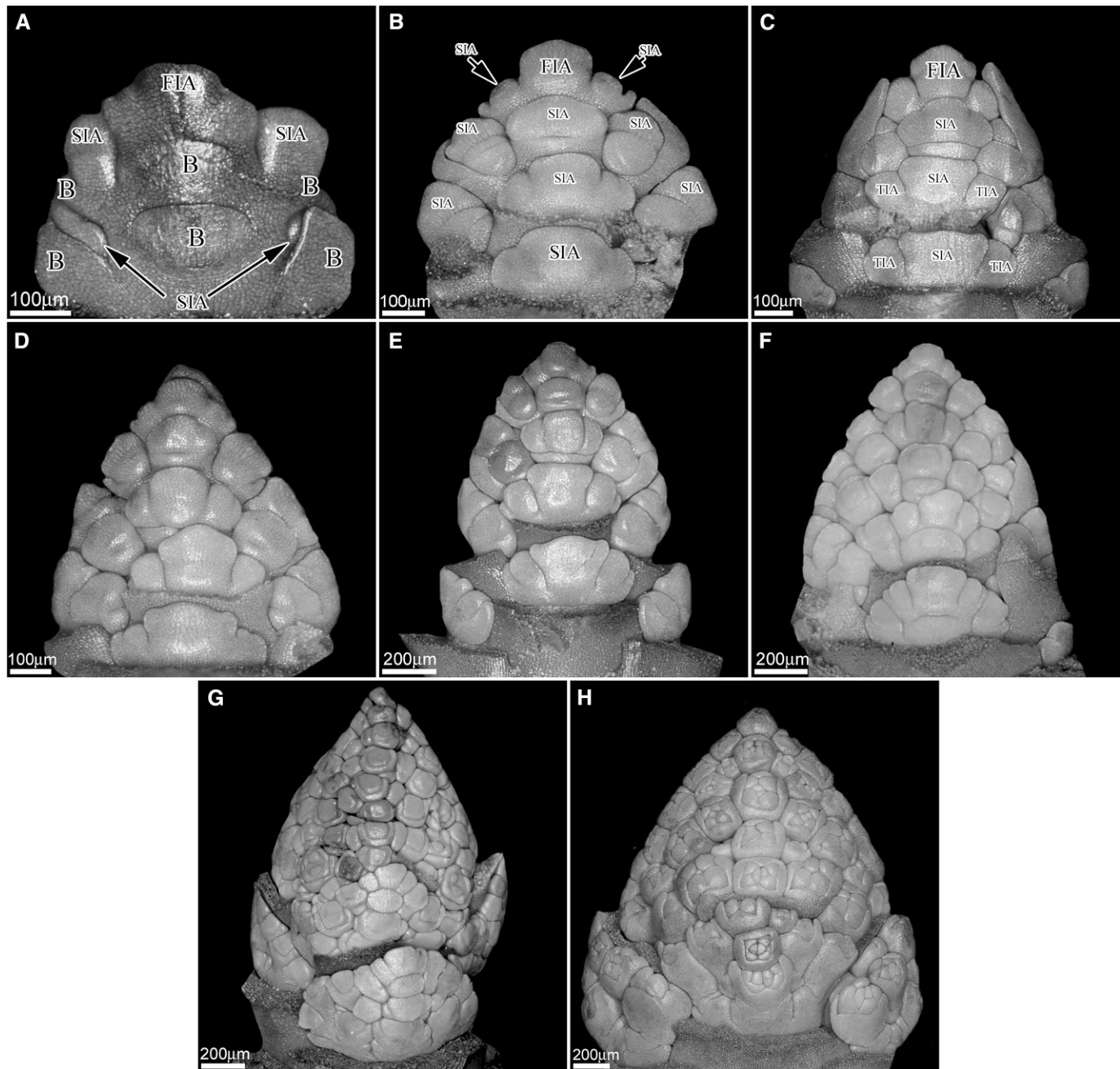


Fig. 9. *Syringa vulgaris*. Inflorescence branching. (A) The first-order inflorescence apex (FIA) produces decussate bracts and second-order inflorescence apices (SIAs) in their axil. (B, C) Second-order inflorescence apices (SIAs) start to produce higher-order branches. (D–G) Side view of different developmental stages showing the progression of branching, which is richer in lower branches. (H) Branching ceases, and the apices of branches of all orders convert into a flower. Abbreviation: B, bract.

into branches. In *Syringa vulgaris*, each lateral bud appears almost simultaneously with its subtending bract so that they appear as a common bract-flower primordium. In general, common primordia tend to occur when growth of the outer of the two components is delayed compared with the inner component. That the bracts are arrested early in development is also reflected by the fact that only some first-order bracts are visible in the mature inflorescence. This behavior was also found in *Chionanthus virginicus*. The lack of obvious bracts for individual

flowers can lead to equivocal interpretations with respect to general architecture and branching pattern of inflorescences. Although flower-subtending bracts are mostly present in inflorescences, there are families in which they are generally lacking, such as Brassicaceae (Hagemann, 1963), Araceae (Buzgo, 2001), Hydatellaceae (Rudall et al., 2007), and Nymphaeaceae (Endress and Doyle, 2009), or they may be present for flowers but lacking for partial inflorescences, such as in Poaceae (Vegetti and Weberling, 1996).

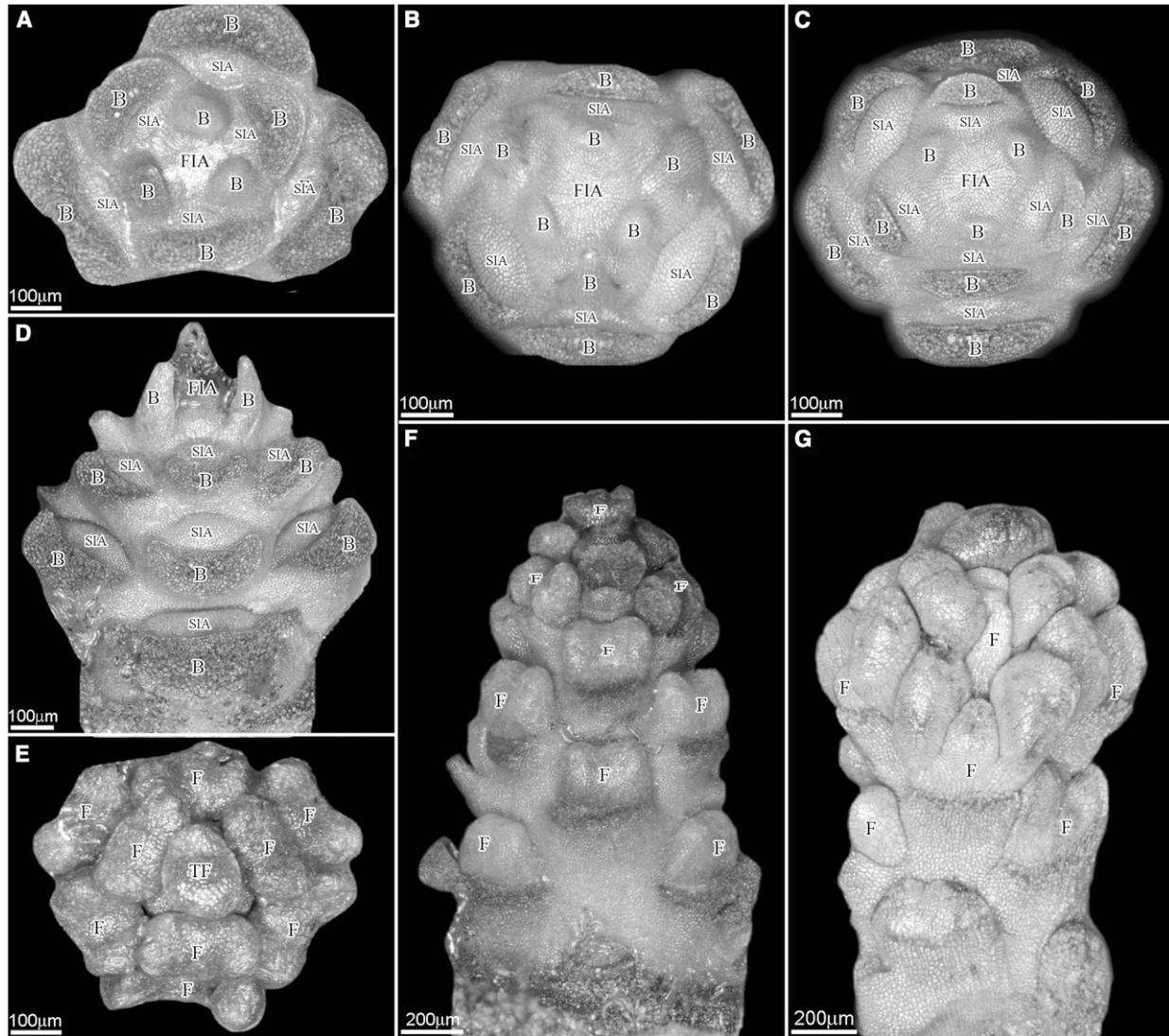


Fig. 12. *Fraxinus excelsior*. Inflorescence development. (A–C) The first-order inflorescence apex (FIA) produces bracts and second-order inflorescence apices (SIAs) in their axils in a tricussate arrangement. (D–F) The FIA and SIAs convert into a flower without further branching. Abbreviations: B, bract; F, flower.

some eudicots, such changes between decussate and tricussate are relatively common in the vegetative region, sometimes even within individuals (e.g., Sitte, 1957). Tricussate patterns are also known in mutants of basically decussate species (Matkowski and Adler, 1999). Spiral phyllotaxis is the most common arrangement of organs in the vegetative region of flowering plants (Jean, 1994; Lyndon, 1998). The change from whorled to spiral or from spiral to whorled phyllotaxis is common at the transition to flowering and sometimes within a flower (Staedler et al., 2007; Staedler and Endress, 2009). Likewise, evolutionary transitions between whorled and spiral patterns in the vegetative region, and in some angiosperm groups even in flowers, are common (Endress and Doyle, 2007). Among the species studied, only *Jasminum fruticosum* has spiral phyllotaxis of flower-subtending bracts. Furthermore, this feature is only present in a minority of species of the genus (Green and Miller, 2009), none of which are included in the phylogenetic trees of Wallander and Albert (2000) and Kim and Kim (2011). The predominance of decussate phyllotaxis in the

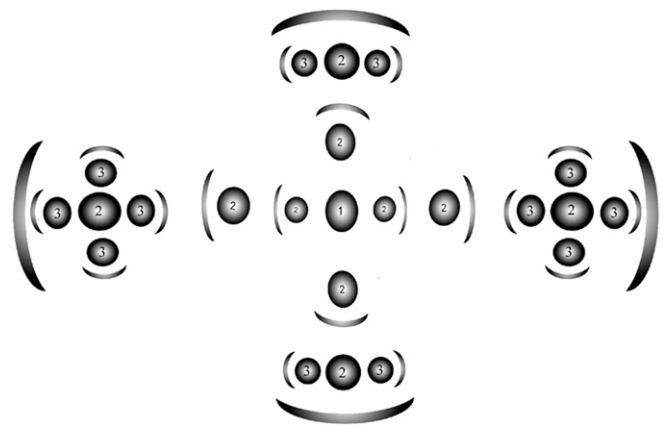


Fig. 13. *Olea europaea*. Inflorescence diagram. Flowers are numbered according to their branching orders.

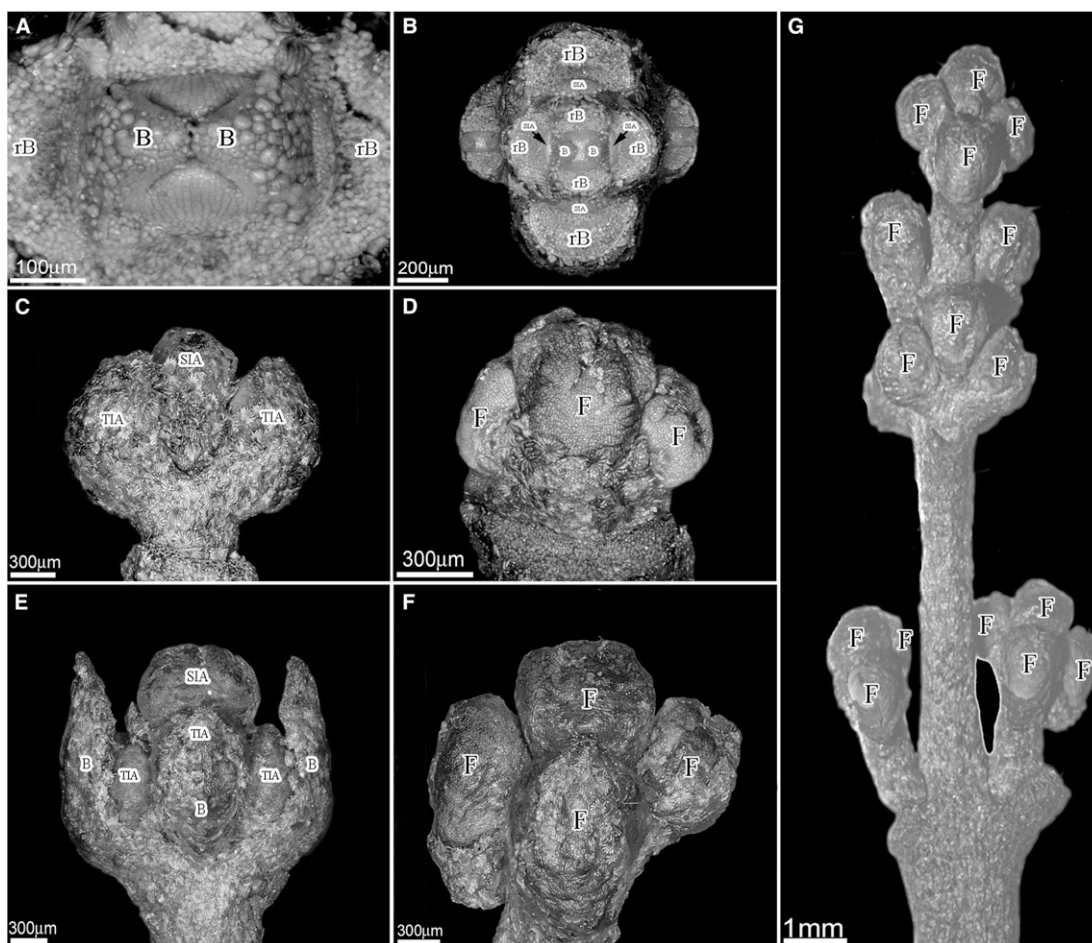


Fig. 14. *Olea europaea*. Inflorescence development. (A, B) The first-order inflorescence apex (FIA) produces decussate bracts and second-order inflorescence apices (SIAs) in their axils. (C, D) Second-order inflorescence apex (SIA) with two bracts and third-order inflorescence apices (TIAs) (or flowers) in their axils. (E, F) SIA with four bracts and TIAs (or flowers) in their axils. (G) The FIA converts into a flower in an advanced inflorescence. Basal branches undergo further branching; upper branches convert into a single flower. *Abbreviations:* B, bract; F, flower; rB, removed bract.

inflorescences of Oleaceae and their outgroups may indicate that this pattern is plesiomorphic in Oleaceae.

Accessory flowers and accessory partial inflorescences—In a number of angiosperms, a pherophyll may bear two or more flowers instead of one. The “supernumerary” flowers arise successively after the first axillary flower and are called accessory flowers (Troll, 1969). The occurrence of accessory flowers has been reported in many families, starting with Amborellaceae, the sister to all other angiosperms (Endress and Igersheim, 2000), and, among Lamiales, for instance in Acanthaceae (Sell, 1969, 1970; Borg and Schönenberger, 2011) and Scrophulariaceae (Weberling and Troll, 1998). Not to be confused with accessory flowers are the so-called front-flowers occurring in the “pair-flowered cymes” of Calceolariaceae, Gesneriaceae, and a few genera of Scrophulariaceae (Weber, 1973, 1982, 2004; Andersson and Molau, 1980; Ehrhart, 2000). These represent distinct lateral branches, the subtending bract of which is usually reduced.

Instead of single accessory flowers, there may also be accessory groups of flowers, so-called accessory partial inflorescences. Such accessory partial inflorescences that are similar in complexity to the inflorescence part with which they are

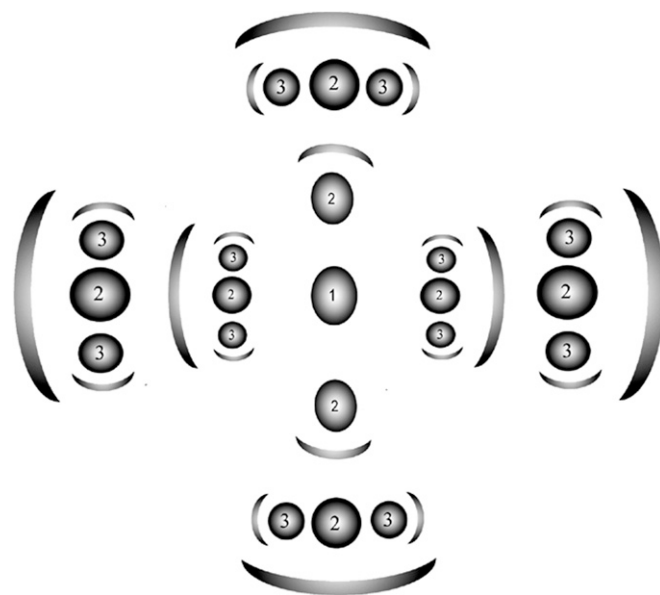


Fig. 15. *Chionanthus virginicus*. Inflorescence diagram. Flowers are numbered according to their branching orders.

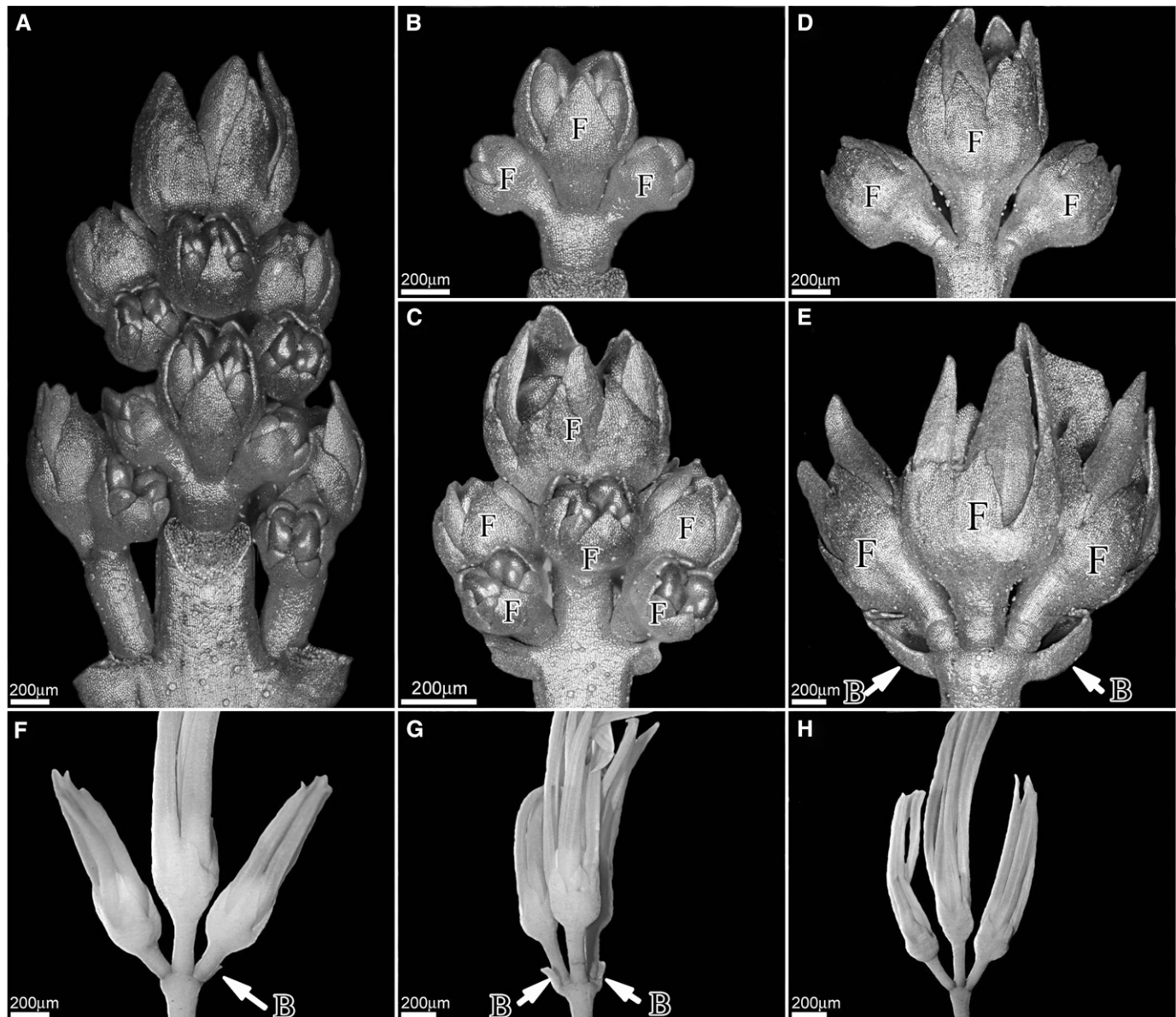


Fig. 16. *Chionanthus virginicus*. Inflorescence development. (A) A developed thyrsoid inflorescence with a determinate main inflorescence axis carrying six cymosely branched second-order inflorescence apices (SIAs). (B) The SIA terminates in a flower after production of two lateral flowers. (C) With removal of the lower branches, the uppermost lateral branch can be seen to convert into a flower without branching. (D) A second-order branch that lacks higher order bracts. (E–H) Different states of bract development (arrows) in some second-order branches. *Abbreviations:* B, bract; F, flower.

associated (Cavalcanti and Rua, 2008) have been described among Lamiales, e.g., in Acanthaceae (*Ruellia*, *Hypoestes*; Sell, 1969, 1970), Gesneriaceae (*Chirita*; Weber, 1975), Plantaginaceae (*Linaria*; Weberling and Troll, 1998), and Scrophulariaceae (*Verbascum*; Weberling and Troll, 1998) and, among other asterids, in Polemoniaceae (*Ipomopsis*) and Rubiaceae (*Coffea*; Weberling and Troll, 1998). In the present study, the occurrence of both accessory flowers and accessory partial inflorescences were observed in *Jasminum fruticans* and *Fontanesia phillyreoides*. In the comparative study on Oleaceae by Troll (1969), neither accessory flowers nor accessory inflorescences were reported. The only mention of accessory flowers in Oleaceae that we found in the literature is a short note for *Abeliophyllum*

(Forsythieae) (Troll, 1964). The distribution of accessory flowers and inflorescences in a number of systematically unrelated families suggests multiple convergent evolution of these formations. However, little is known about their global systematic distribution in angiosperms. They are of potential interest in horticulture or agriculture because they are a means of increasing the number of flowers in an inflorescence without a change in the basic branching pattern.

Systematic and evolutionary aspects—While particular forms of inflorescences are often characteristic for families or other larger clades, the same kind of inflorescence architecture can also be found in many unrelated families. It appears that inflorescence

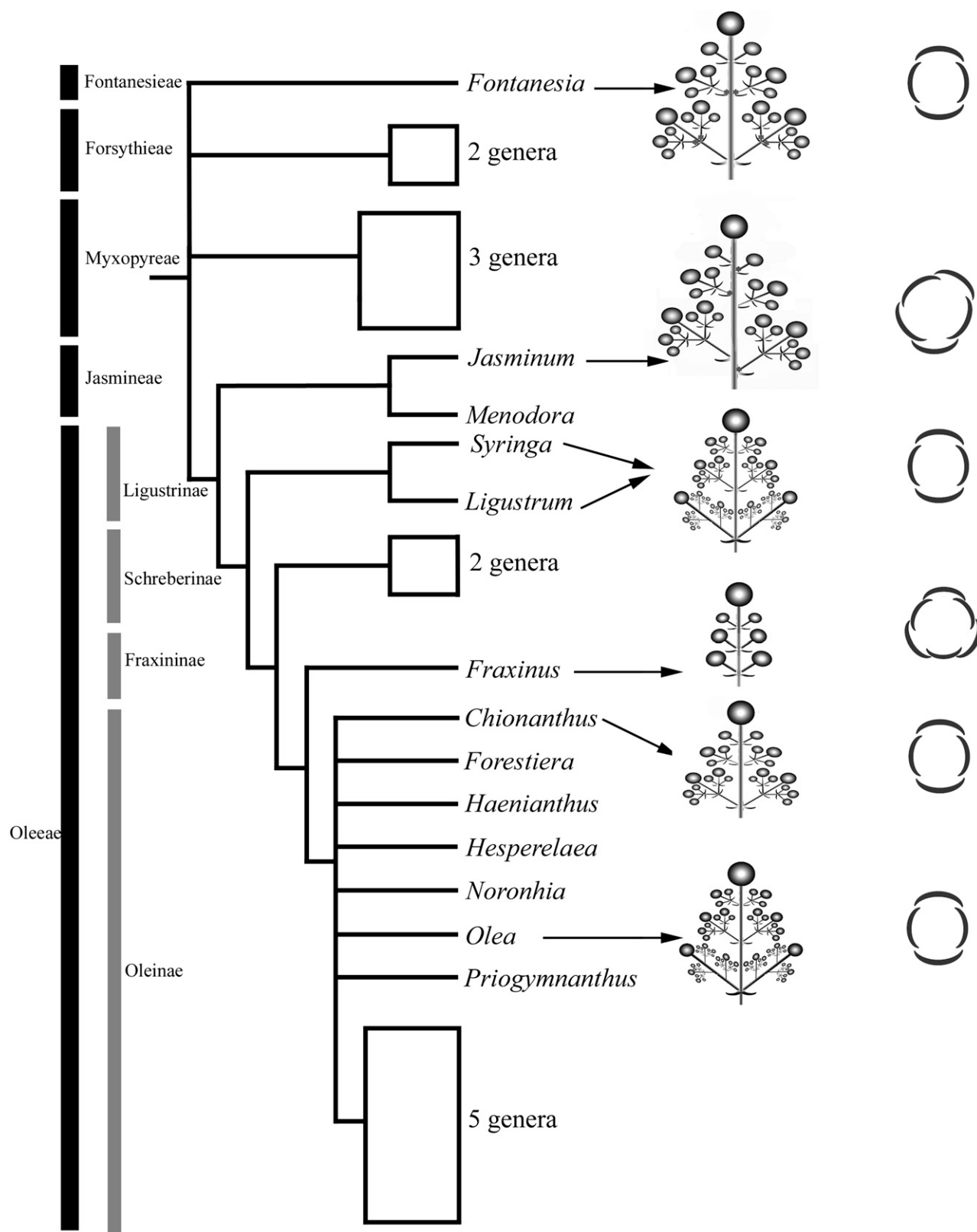


Fig. 17. Phylogenetic tree of Oleaceae (based on the molecular studies by Wallander and Albert, 2000) together with inflorescence branching and phyllotaxis of floral subtending bracts. Accessory flowers are marked with asterisk.

diversity within a specific family is mainly related to the number of flowers or partial inflorescences, the longevity of such units, and the differential length of branches, whereas branching patterns are much less affected (Endress, 2010). Nevertheless, the present study shows a certain variability of branching pattern and phyllotaxis among the studied taxa of Oleaceae and presents some new features related to the development of inflorescences. These features could be of special macrosystematic and comparative morphological interest.

Unfortunately, phylogenetic resolution of the deep nodes within Oleaceae is almost lacking so that only limited discussion about the evolution of features is possible. The most detailed phylogenetic study as yet is that based on *rps16* and *trnL-F* by Wallander and Albert (2000) (Fig. 17). In their study, Fontanesieae, Forsythieae, Myxopyreae, Jasmineae, and Oleaeae form well-supported clades. Jasmineae and Oleaeae are moderately supported sisters. The mutual position of Fontanesieae, Forsythieae, Myxopyreae, and the clade of Jasmineae plus Oleaeae, however, is largely unresolved. At the subtribe level, Ligustrinae, Schreberinae, Fraxininae, and Oleinae form a grade. The study by Kim and Kim (2011) on Forsythieae based on nuclear and plastid data brings some more resolution but the taxon sampling is more restricted (without Myxopyreae). In their study, Jasmineae plus Fontanesieae are sister to Oleaeae plus Forsythieae, which differs from Wallander and Albert (2000).

The occurrence of accessory flowers and accessory partial inflorescences in Fontanesieae and Jasmineae may suggest this to be an apomorphy for a Jasmineae plus Fontanesieae clade (as found by Kim and Kim, 2011), if it is not a plesiomorphy for the family, and then not expressed (or not yet discovered) in other clades. That it may be a plesiomorphy is indicated by the fact that it is known from a number of other families in Lamiales.

Among Oleaeae, subtribe Ligustrinae includes two genera, *Syringa* and *Ligustrum*. In both genera, the branching pattern and phyllotaxis is the same and is represented by a decussate paniculate inflorescence (with poor branching in the upper phyll axils of each branch and therefore approaching compound botryoids). This branching pattern supports the close relationship of the two genera. However, the inflorescence of *Syringa vulgaris* differs from that of *Ligustrum vulgare* and other studied taxa by the formation of common bract-flower primordia and the reduction of higher-order bracts.

The only representative of Fraxininae here studied, *F. excelsior*, differs from other studied taxa in its branching pattern and subtending floral bract phyllotaxis. A racemose pattern (botryoid) and tricussate flower arrangement were found only in *Fraxinus*. Richly branched inflorescences of *F. excelsior*, however, may also be paniculate (Troll, 1969).

On the other hand, *Olea europaea* and *Chionanthus virginicus* (both Oleinae), show the most common decussate arrangement as Ligustrinae. The paniculate inflorescences (approaching compound botryoids) of *Olea* are also comparable with those of Ligustrinae. The presence of panicles (approaching compound botryoids) in some representatives of Oleaeae favors the view that this pattern is a derived condition that possibly originated from a thyrsoïd pattern, which is concentrated in the other tribes. It appears that in Fontanesieae and Jasmineae increase in flower number per inflorescence is achieved by the formation of accessory flowers and accessory partial inflorescences, whereas in Oleaeae flower number is increased by changing from simple thyrsoïds to compound thyrsoïds.

Conclusions—The results of this study show diversification in branching patterns and phyllotaxis among the studied taxa of Oleaceae. We described the formation of common bract-flower primordia, the suppression of bracts, and the occurrence of accessory flowers and accessory partial inflorescences, which are not predictable from the external morphology of mature inflorescences. Future studies need to work out potential relationships among these features. Both the evolution of accessory flowers/partial inflorescences and the change from simple to compound thyrsoïds are a potential means to increase the number of flowers in inflorescences of Oleaceae. It would be interesting to know which pathway is easier to influence in experimental studies. More taxa are needed for study to fill in the gaps and to achieve a broader understanding of the evolutionary dynamics of inflorescences in this large and horticulturally and agriculturally important plant family, once its phylogeny is better resolved.

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